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THE CONSEQUENCES OF CHANGING THE TOP PREDATOR IN A FOOD WEB: A COMPARATIVE EXPERIMENTAL APPROACH

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Abstract. Changing the top predator in a food web often results in dramatic changes in species composition at lower trophic levels; many species are extirpated and replaced by new species in the presence of the new top predator. These shifts in species composition also often result in substantial alterations in the strengths of species interactions. However, some species appear to be little affected by these changes that cause species turnover at other positions in the food web. An example of such a difference in species responses is apparent in the distributions of coenagrionid damselflies (Odonata: Zygoptera) among permanent water bodies with and without fish as top predators. *Enallagma* species segregate between ponds and lakes that do and do not support fish populations, with each lake type having a characteristic *Enallagma* assemblage. In contrast, species of *Ischnura*, the sister genus to *Enallagma*, are common to both fish and fishless ponds and lakes. Previous research has shown that *Enallagma* species segregate because they are differentially vulnerable to the top predators in each lake type: dragonflies in fishless lakes and fish in fish lakes. This paper reports the results of a series of laboratory and field experiments quantifying the mortality and growth effects of interactions in the food webs surrounding *Enallagma* and *Ischnura* species in both lake types. These results are compared to determine how features of the food web change to force segregation of *Enallagma* species between the lake types but permit *Ischnura* species to inhabit both.

The results of experiments conducted in a fishless lake show that damselflies are not food limited in this lake type, but that they do strongly compete via interference mechanisms. Interference effects between the genera are symmetrical. *Ischnura* species have substantially higher growth rates than *Enallagma* species under all conditions in fishless lakes. Although both *Enallagma* and *Ischnura* experience substantial mortality from predation by dragonflies (*Anax* and *Aeshna* species, the top predators in fishless lakes), these dragonflies display a significant bias towards feeding on *Ischnura.* Mortality rates due to dragonfly predation are not density dependent. The results of experiments done in a fish lake indicate that damselflies are food limited and thus compete for resources in fish lakes. *Ischnura* growth rates are also substantially higher than *Enallagma* species in the fish-lake system. Dragonfly species that coexist with fish (*Basiaeschna* and *Epitheca* species) do not impose significant mortality on coexisting damselflies, but they do compete for resources with the damselflies, and they may also generate feeding interference in the damselflies. Fish impose significantly higher mortality on *Ischnura* species than on coexisting *Enallagma* species, and this mortality is negatively density dependent.

The coexistence of *Enallagma* and *Ischnura* species is fostered in both lake types by trade-offs in their abilities to avoid predators and to utilize resources. Native *Enallagma* species are better at avoiding coexisting predators in each lake type, but these abilities come at the expense of the ability to utilize resources effectively and to avoid the predator found in the other lake type. In contrast, *Ischnura* are better at utilizing resources in both lake types, but these abilities come at the expense of effectively avoiding both fish and dragonflies. Understanding the trade-offs faced by species at similar trophic positions within a food web is critical to predicting changes in food webs following major environmental perturbations such as changing the top predator.

Key words: coexistence; community structure; density dependence; Enallagma; *food limitation; food web;* Ischnura; *Odonata; predation; resource competition; trade-offs; trophic structure.*

INTRODUCTION

Understanding how community structure is altered by dramatic environmental changes is a major focus in ecology. These efforts are motivated by comparisons of natural communities existing at different points along environmental gradients that generate these dramatic changes (e.g., intertidal zonation patterns [Connell 1961, Paine 1966, 1974, Lubchenco 1978, 1980], lakes with different numbers of trophic levels [Brooks and Dodson 1965, Dodson 1970, 1974, Sprules 1972, Zaret 1980, Vanni 1986, 1988, McPeek 1989, 1990*a*,

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Persson et al. 1992, Arnott and Vanni 1993], and terrestrial and lake communities along nutrient gradients [Tilman 1982, 1988, McQueen et al. 1986, 1989]). Much of current theory explores the consequences of these dramatic ecological changes using models that assume that whole trophic levels respond as units (e.g., Fretwell 1977, Oksanen et al. 1981, 1992, McQueen et al. 1986, 1989, Ginzberg and Akçakaya 1992, Hunter and Price 1992, Power 1992, Carpenter and Kitchell 1993) or assume that all species at a given trophic level are similarly affected by these changes (e.g., Hairston et al. 1960, Menge and Sutherland 1976, 1987).

Although these models have made tremendous contributions to stimulating thought and empirical research, they tend to blur important differences between species within a given trophic level. Natural communities have many species at similar trophic positions (Winemiller 1990, Polis 1991), and each may respond quite differently to the same perturbation (e.g., Berquist and Carpenter 1986, Vanni 1987, Leibold 1989, 1991, Wootton 1992, 1994). Also, comparisons of assemblages in different communities indicate that major environmental changes can lead to the extirpation and replacement of some species but leave other species at the same trophic level largely unaffected (see papers cited in the first paragraph of the *Introduction,* above). Expanding current theoretical constructs to address differences in species responses within a given trophic level will provide much greater power for predicting changes in food web interactions associated with major environmental perturbations.

In this paper I examine why different damselfly genera inhabiting littoral lake communities respond differently to alterations in food web interactions caused by changing the top predator. Characteristic species assemblages for most taxa exist over different ranges along the gradient of permanence from small, vernal ponds to large, permanent lakes (see recent reviews by Wellborn et al. 1996, Skelly 1997). Damselflies in the family Coenagrionidae (Odonata: Zygoptera) are mid-trophic level consumers in the littoral food webs of marshes, ponds, and lakes at the permanent end of this environmental gradient. Coenagrionid damselflies are restricted to relatively permanent water bodies, because they require 10–11 mo to complete the aquatic phase (egg and larva) of their life cycle. One group of species in the genus *Enallagma* is found as larvae only in fish-free water bodies, whereas the remaining *Enallagma* species are found as larvae only in water bodies that support fish populations (Johnson and Crowley 1980, McPeek 1989, 1990*a*). In contrast, larvae of *Ischnura* species, the sister genus of *Enallagma* (J. M. Brown and M. A. McPeek, *unpublished manuscript*), are common in both lake types (Johnson and Crowley 1980, McPeek 1990*a*).

Previous work indicates that the differential vulnerabilities of *Enallagma* species to fish and dragonfly predators are primarily responsible for their segregation between the two lake types (Pierce et al. 1985, Blois-Heulin et al. 1990, McPeek 1990*a, b*). Many larger ponds, marshes, and lakes that are relatively permanent in their persistence (drying on a time scale of decades or centuries) lack fish, because these water bodies lack inlet and outlet streams to serve as routes of fish colonization or because fish are excluded by the abiotic conditions of the waters (e.g., low winter oxygen concentrations) (Tonn and Magnuson 1982, Rahel 1984). In these fishless waters, large, active dragonfly species (e.g., *Anax, Aeshna,* and *Tramea* species) are the top predators in the littoral food web, and dragonfly predation excludes *Enallagma* species that are found only coexisting with fish (McPeek 1990*a*). (Hereafter, I will refer to these permanent ponds and lakes without fish as dragonfly lakes, because of dragonflies' pivotal role in setting species composition.) Likewise, fish are the top predators in fish lakes, and fish predation excludes *Enallagma* species that are found only in dragonfly lakes (McPeek 1990*a*). Fish predation also causes the assemblage of large, active dragonflies found in dragonfly lakes to be replaced by an assemblage of smaller and less active dragonfly species (e.g., *Basiaeschna, Epitheca,* and *Celithemis* species) in fish lakes (Hall et al. 1970, Johnson and Crowley 1980, Crowder and Cooper 1982, Morin 1984*a, b*, Pierce 1988, McPeek 1990*a*, Werner and McPeek 1994). Interestingly, a third group of dragonflies (e.g., *Erythemis* and *Pachydiplax* species) are, like *Ischnura,* found in both lake types (Johnson and Crowley 1980, McPeek 1990*a*). Dragonfly predation in fish lakes, abiotic factors, and competitive interactions between *Enallagma* species do not contribute to maintaining the segregation of *Enallagma* species (Pierce et al. 1985, McPeek 1990*a*).

The study presented here was designed to reveal why *Enallagma* and *Ischnura* species are differentially affected by changing the top predator in the littoral food web by comparing the types and strengths of interactions affecting their mortality and growth in dragonfly and fish lakes. *Enallagma* and *Ischnura* species have similar diets (Pearlstone 1973, Thompson 1978, Johnson et al. 1984), and their growth rates have been shown to decrease as damselfly densities increase (Johnson et al. 1984, Anholt 1990, McPeek 1990*a*). This suggests that in each lake type *Enallagma* and *Ischnura* species face the same predators and may compete for the same resources. Theory predicts that coexistence of such species should be facilitated by trade-offs in their abilities to engage in these interactions; the likelihood of coexistence is enhanced if some species are better adapted to avoiding predators and thereby suffer lower mortality due to predation, but other species are better adapted to utilizing resources and thereby have higher growth or fecundity (Levin 1970, Phillips 1974, Vance 1978, Leibold 1989, 1996, Holt et al. 1994, McPeek 1996*a*). Therefore, in each lake type one genus should have higher fitness components associated with predator avoidance, while the other should have higher fitness components associated with better resource utilization abilities.

Can theory also suggest which roles *Enallagma* and *Ischnura* are expected to fill in each lake type? Substitution of one top predator for another will most likely remove the advantage enjoyed by species that are better adapted to predator avoidance; species occupying this position in the food web with one top predator are expected to be extirpated and replaced by other species that are well adapted to avoiding the new top predator (McPeek 1996*a*). In contrast, species that are effective at exploiting resources but poor at avoiding various types of predators may often be capable of existing in both communities, if positions for such species are available in the food webs of both communities (McPeek 1996*a*). Given the distributions of *Enallagma* and *Ischnura* between dragonfly and fish lakes, these theoretical considerations predict that in each lake type *Enallagma* species should experience lower mortality due to predation than *Ischnura,* but in both lake types *Ischnura* should utilize resources more effectively to give them higher growth rates than the native *Enallagma.*

To test these predictions, I performed a series of complementary laboratory and field experiments to quantify the interactions affecting *Enallagma* and *Ischnura* in the two lake types. Duplicate sets of experiments were performed in the two lake types to quantify the relative strengths of competition within and between the two genera, the degree of resource limitation, and the impacts of predators on the survival and growth of native *Enallagma* and *Ischnura.* This type of study has been called a "comparative experimental approach" (Lubchenco and Real 1991, Menge et al. 1994). This approach has many advantages over other possible study designs (e.g., adding fish to a previously fishless lake): (1) because the rate of change from one community type to the other after adding or removing a top predator will be largely determined by how fast missing species colonize experimental units, many problems with lengthy transient dynamics are alleviated; (2) experiments are done in a natural background of abiotic conditions and species composition for each system; and (3) most importantly the interactions are being compared in well-developed, natural systems.

MATERIALS AND METHODS

Field abundance

To quantify the distributions of *Enallagma* and *Ischnura* species, I sampled larval damselfly densities in three dragonfly lakes and three fish lakes during September and October 1987. Because abundances of littoral invertebrates vary with the structural complexity of the macrophytes in which they are sampled (Cyr and Downing 1988, Rasmussen 1993, Lalonde and Downing 1992), I sampled only lakes dominated by the macrophyte *Chara vulgaris* in order to standardize density estimates to a common level of structural complexity. I used a 20 cm diameter section of stovepipe covered at one end by two layers of mosquito netting (0.6 × 1.2 mm mesh) (McPeek 1990*a*). Samples were taken by plunging the open end of the stovepipe through the *Chara* into the sediment, sealing the bottom end with a plexiglass plate, and placing the entire contents in a bucket. Samples were returned to the laboratory and sieved through 5.7 mm and 0.5 mm mesh sieves to remove large plant material and sediment. All damselflies were then picked alive from the samples. Five to six samples were taken in each lake at positions chosen haphazardly in water 0.25 to 0.75 m deep.

Laboratory feeding bias

I evaluated the feeding biases of fish and dragonfly predators characteristic of each lake type in the laboratory: *Aeshna mutata* dragonflies from dragonfly lakes, and bluegill sunfish (*Lepomis macrochirus*) and *Epitheca cynosura* dragonflies from fish lakes. *Aeshna* is a common dragonfly that is restricted to dragonfly lakes, and *Epitheca* is most common in fish lakes (Johnson and Crowley 1980, McPeek 1990*a*). Bluegill sunfish are the dominant fish foraging in the littoral zones of lakes in southwestern Michigan, where this study was conducted (Brown and Ball 1942, Cooper et al. 1971, Werner et al. 1977, Werner and Hall 1988). All three of these predators display feeding biases similar to those of other fish and dragonflies, respectively (McPeek 1990*a*). The methods used here closely followed those of McPeek (1990*a*).

Feeding trials involving dragonflies were performed in 20 cm diameter circular dishes filled to a depth of 6 cm with tap water. The dishes were bare except for a layer of fiberglass window screening covering the bottoms to provide footing for the odonates. (Trials in which the macrophyte *Chara vulgaris* was added to dishes to provide structural complexity gave similar results [McPeek 1990*a*].) For each of 12 trials involving *Aeshna mutata,* five *Enallagma boreale,* and five *Ischnura verticalis* larvae taken from a dragonfly lake, were added to a dish and allowed to acclimate for 3–5 h. One final-instar *Aeshna* larva was then added to each dish and allowed to feed until it had eaten roughly half the larvae or until satiated, whichever came first; most trials lasted 30–45 min. For each of eight trials involving *Epitheca cynosura,* five *Enallagma signatum,* and five *Ischnura verticalis* larvae taken from a fish lake, were added to a dish and allowed to acclimate for 3–5 h. Then one final-instar *Epitheca* larva was added to each dish and allowed to feed for 2 d (*Epitheca* are much less active than *Aeshna* and consequently feed at much slower rates). No larvae were killed during the acclimation periods when dragonflies were absent, indicating that death due to damselfly predation was minimal during these trials. No dragonfly or damselfly was used in more than one trial.

Trials using bluegill sunfish (75–85 mm Standard Length [SL]) were performed in 38-L aquaria. A thin layer of the macrophyte *Chara vulgaris* was added to each aquarium to provide some structure. For each of nine trials, eight *Enallagma signatum* and eight *I. verticalis* larvae from a fish lake were added to an aquarium and allowed to acclimate for 3–5 h. One fish was then added to each aquarium, allowed to feed for 24 h and removed, and the contents of the aquarium was sorted to recover all uneaten damselflies. No fish or damselfly was used more than once.

Predator feeding biases were evaluated using Manly's index of preference calculated for *Ischnura* larvae (Manly 1974, Chesson 1983). Manly's index (α_I) ranges in value from 0.0 to 1.0. A value of $\alpha_I = 0.5$ indicates the predator shows no bias towards either prey; $\alpha_I > 0.5$ indicates that the predator feeds disproportionately on *Ischnura* larvae.

Field experiments

General methods.—In 1993, the dragonfly-lake field experiments were performed in Pond 3 (a fishless pond of area ~1 ha) on the Lux Arbor Reserve of the Kellogg Biological Station (KBS), Barry County, Michigan, USA. Because of a severe blue-green algal bloom in this pond in the summer of 1994, the remaining set of dragonfly-lake experiments were performed in 1995 in another fishless pond on the Lux Arbor reserve, Gravelpit Pond, of area ~0.25 ha.

All field experiments requiring a lake with fish were performed in Palmatier Lake (Barry County, Michigan, USA), an ~6 ha lake that contains a diverse fish assemblage. Bluegill sunfish are the dominant fish preying on littoral zone invertebrates in this lake (Osenberg et al. 1988, Mittelbach and Osenberg 1993), and *Chara vulgaris* was the dominant submerged macrophyte growing in the littoral zone (M. A. McPeek, *personal observation*).

The methods used in these experiments closely followed those used in previous studies (e.g., McPeek 1990*a*). Experiments involving no predators or dragonfly predators were done in smaller cylindrical cages (30 cm diameter, 1.2 m high, bottom area 0.073 m^2); experiments involving fish were done in larger cylindrical cages (54 cm diameter, 1.2 m high, bottom area 0.224 m^2). All cages were cylinders of 2 cm mesh chicken wire covered with mosquito netting (0.6 × 1.2 mm mesh size) and sealed at the bottom ends with plastic dishes containing ~2 cm of sediment. The tops of cages extended out of the water and were uncovered. All cages in an experiment were linearly arranged in 0.6–0.8 m deep water. *Chara vulgaris* was added to each cage in natural density. In the absence of predators, damselflies have similar growth and mortality rates in the two cage sizes, and growth and mortality rates in the presence of predators are quite similar to rates in natural populations (McPeek 1990*a*).

All experiments were initiated in late August after damselfly species used in the experiments were too large to pass through the mosquito netting, except in three cases. This procedure minimizes contamination of cages by damselflies (McPeek 1990*a*). To initiate an experiment, all cages were installed in the lake, *Chara* was added, and then the cages were allowed to stand for ~1 week prior to the addition of damselflies or the application of treatments. This allows colonization by small organisms, which are prey for damselflies and their predators, through the mosquito netting. Chironomids, littoral cladocerans, littoral copepods, ephemeropterans, annelids, and amphipods were all abundant at the end of experiments. Replicates of treatments were always randomly assigned to cages. Experiments were generally terminated in early to mid October.

Damselfly larvae used in experiments in the dragonfly lake were collected from fishless water bodies near KBS. Larvae were collected from ponds other than those used for experiments, because collection damages macrophyte beds in the vicinity of the collection, and I was concerned that this disruption in a small pond might influence the results of experiments. *Enallagma* larvae for experiments in the dragonfly lake were collected from Marshfield Road Marsh, a large fishless marsh just north of KBS. These larvae were a mixture of *E. boreale* and *E. cyathigerum*; these two species will be treated as a single taxon in this study, because they are nearly indistinguishable as larvae, they cooccur in all dragonfly lakes used in this study, and they are also very similar in behavior and morphology (McPeek 1989 and *unpublished data*). Hereafter, I will refer to them together as *E. boreale,* because *E. boreale* constituted >90% of the larvae at Marshfield Road Marsh where these species were collected for experiments (M. A. McPeek, *unpublished data*). *I. verticalis* larvae were collected from a number of fishless ponds at the Experimental Pond Laboratory of KBS. (*I. verticalis* is also difficult to distinguish from the closely related *I. posita* as very small larvae. Nearly all larvae recovered from cages in the field experiments (>98%) were *I. verticalis.*)

Damselfly larvae used in experiments in the fish lake were collected from Palmatier Lake, but in areas distant from where experiments were established. Two to three *Enallagma* species were usually included in experiments in fish lakes to mimic the diverse *Enallagma* assemblage found in fish lakes in North America (e.g., 11 *Enallagma* species coexist in Palmatier Lake, with three species predominating), but different combinations of species were used in different experiments. This was necessitated by the availability of various species at the times when experiments were established. *I. verticalis* larvae were used in all experiments.

Larvae were assigned randomly by species to the different replicates of an experiment. Larvae were added in the natural size distribution available at the start of the experiment; this meant that for most species, larvae in a narrow range of 2–3 instars were added (damselflies have 11 instars total). A sample of 20–30 larvae of each species was preserved in 10% neutral formalin to characterize the initial size distribution added to each experiment.

At the end of an experiment, the contents of cages (except sediment) were returned to the laboratory where they were sieved through sieves of 5.7 mm and 0.5 mm mesh to remove large plant material and residual sediment. All damselflies, dragonflies, and fish were immediately removed from the sieved samples alive and then preserved in 10% neutral formalin. The head widths of all recovered larvae were measured with a dissecting microscope fitted with an ocular micrometer. All larvae were then dried in a 60°C drying oven for >24 h and individually weighed to determine their dry body mass. When preserved in formalin, damselflies often lose their caudal lamellae. Therefore, the caudal lamellae of all larvae were removed before drying.

When the experimental design permitted, multivariate analyses of variance (MANOVA) with a priori, orthogonal contrasts were performed on the mortality and growth rates of all species in cages using the GLM procedure of SAS (SAS 1990). A mortality rate was calculated for each species in each cage in an experiment using mortality rate = −(ln[number recovered] − ln[initial number])/(duration of experiment), where "ln" signifies natural logarithm. This equation assumes a constant mortality rate throughout the experiment (i.e., $N(t) = N(0)\exp(-dt)$, where d = mortality rate, $N(0)$ is the number of larvae added to a cage, $N(t)$ is the number of larvae recovered, and t is the duration of the experiment in days), and this mortality rate (larval deaths per larva per day) is expressed in units of d^{-1}. A growth rate was also calculated for each species in each cage in the experiment. To calculate growth rate, the dry masses of recovered larvae were natural-log transformed, and a mean ln of larval dry mass was calculated for the cage. The growth rate was calculated by growth rate = ([mean ln M of recovered larvae] − [mean ln M of larvae in initial sample])/(duration of experiment in days), and is expressed in units of d^{-1}, where M is dry mass. This metric of growth rate assumes a model of $M(t) = M(0)\exp(gt)$, where g is the growth rate and is independent of the initial sizes of species. The F-approximation of Wilks' lambda is reported for results of MANOVA. When necessary, based on the results of the MANOVA, variables for each species were analyzed separately using univariate analyses of variance to determine which variables and species contributed to the overall MANOVA treatments effects. All statistical tests for field experiments are two-tailed.

TABLE 1. Design of the Intra- vs. Intergeneric Competition Experiment in a study of the effects of changes in the upper levels of a lake food web. An × is placed in each of the nine density combinations included in this experiment.

Number of *Ischnura* added	Number of *Enallagma* added: 0	15	30	45
0		×	×	×
15	×	×	×	
30	×	×		
45	×			

Four experiments were performed in the dragonfly-lake system, and six experiments were performed in the fish-lake system. Two experiments in each lake type quantified the strengths of competitive interactions among the damselflies in the absence of predators and the degree of food limitation. Two experiments were also performed in each lake type to quantify interaction strengths among damselflies and native dragonfly predators, and the degree to which mortality and growth of damselflies in the presence of dragonflies depended on damselfly density. Two experiments also addressed these issues using fish predators in the fish-lake system. In the following I describe the rationale and designs of these duplicate experiments.

Intrageneric vs. intergeneric competition.—These experiments were designed to quantify competition among *Enallagma* and *Ischnura* species in the absence of predators. The same basic design was duplicated in each lake type in 1993. Twenty-seven cages were installed in a lake, and following the 1-wk prey colonization period damselfly larvae were added to cages in the density combinations given in Table 1. In this experimental design, three total damselfly abundances were established (i.e., 15, 30, and 45 larvae/cage), and the relative abundances of *Enallagma* and *Ischnura* were manipulated within each total abundance. This experiment was designed to quantify competitive interactions between the two genera; it was not designed to partition competitive effects among species within each genus. Three replicates of each density combination were performed. The natural density for this water volume at this time of year would be equivalent to ~50 larvae/cage. These densities were chosen because previous experiments have shown that competitive effects on growth are detected at densities well below natural (generally <25 larvae/cage), but growth rates do not continue to decline as density is increased above natural densities (McPeek 1990*a*).

In the experiment done in the dragonfly lake *Enallagma boreale* and *I. verticalis* were used, and the experiment was terminated after 43 d. In the experiment done in the fish lake, *E. geminatum* and *E. vesperum* comprised the *Enallagma* added to cages: for the 15 *Enallagma* treatments, eight *E. vesperum* and seven *E. geminatum* were added; for the 30 *Enallagma* treatments, 15 of each were added; and for the 45 *Enallagma* treatments, 23 *E. vesperum* and 22 *E. geminatum* were added. The fish-lake experiment was terminated after 40 d.

Because larvae of one or the other species were missing from some treatments, an overall MANOVA could not be performed on this design. Separate MANOVAs were therefore performed on growth and mortality rates for each species in each experiment.

Density manipulation in the presence of dragonflies.—These experiments test whether dragonflies impose density-dependent mortality on the damselflies, and whether damselflies compete in the presence of dragonflies. The same basic experimental design was duplicated in each lake type in 1993. Nine 30 cm diameter cages were installed in a lake, and after the prey colonization period, three total damselfly density treatments of 15, 45, or 90 total damselflies/cage were established, with three replicates/treatment. These densities bracketed natural density (~50 larvae/cage). The relative abundances of species initially present in cages were held constant across the density treatments.

In the dragonfly-lake experiment, the relative abundances of the two species added to cages were held constant across the total density treatments at a ratio of 2:1 *Enallagma boreale* : *Ischnura verticalis.* One penultimate instar *Anax junius* dragonfly larva (Anisoptera: Aeshnidae) was added to each cage 8 d after the damselflies were added, and the experiment was terminated after 35 d.

In the fish-lake experiment, equal numbers of *I. verticalis, Enallagma vesperum* and *E. geminatum* were initially present in each cage. One penultimate instar *Basiaeschna janata* dragonfly larva (Anisoptera: Aeshnidae) was added to each cage 3 d after the damselflies were added, and the experiment was terminated after 30 d.

Dragonfly densities are near natural for these species in their respective lakes (McPeek 1990*a*).

Density manipulation in the presence of fish.—This experiment is analogous to the previous pair involving dragonflies, but tests whether fish impose density-dependent mortality on the coexisting damselflies, and whether the coexisting damselflies compete in the presence of fish. Six 54 cm diameter cages were installed in the fish lake in 1995, and following the 1-wk prey colonization period, two total damselfly density treatments of 45 and 225 total damselflies/cage were established, with three replicates/treatment. These densities bracketed the natural density for the cage size used (~150 larvae/cage). In each treatment, *Enallagma vesperum* initially comprised 55.6% of the larvae, *E. geminatum* initially comprised 22.2%, and *I. verticalis* initially comprised 22.2%. One bluegill sunfish (*Lepomis macrochirus*) (75–80 mm SL) was added to each cage 3 d after the damselflies were added; this fish density is within the natural range for lakes in southwestern Michigan (Mittelbach 1988). This experiment was terminated after 44 d.

Food addition.—Two experiments were performed in 1995 to evaluate whether damselfly mortality and growth rates are limited by food availability in either lake type. In the dragonfly lake, two total damselfly density treatment levels ([1] 15 *Enallagma boreale* and 7 *I. verticalis* or [2] 45 *E. boreale* and 21 *I. verticalis*) were cross-factored with two levels of food addition ([1] no food added, [2] food added). Four replicates per treatment combination were performed. This experiment was terminated after 51 d.

Results of the Density Manipulation in the Presence of Dragonflies experiment done in the fish lake indicated that competitive interactions among damselflies are more pronounced in the presence of dragonflies (see *Results*). Therefore, the experiment done in the fish lake to test for food limitation was designed to incorporate both damselfly density and dragonfly predator effects. Three damselfly abundance/dragonfly treatments ([1] low damselfly density and dragonflies absent, [2] high damselfly density and dragonflies absent, and [3] high damselfly density and dragonflies present) were cross-factored with two levels of food addition ([1] no food added, [2] food added) in this experiment. Three replicates per treatment were performed. Low damselfly density treatments initially had 20 damselfly larvae present; high damselfly density treatments initially had 80 damselflies present (natural density ≈50 larvae/cage). In this experiment, *Enallagma geminatum* and *E. vesperum* were used. In all cages *I. verticalis* initially comprised 26.7% of damselflies, *E. geminatum* 21.3%, and *E. vesperum* 52.0%. Four penultimate instar *Epitheca cynosura* larvae (Anisoptera: Libellulidae) were added to each cage in the "High Damselfly Density and Dragonflies Present" treatment combinations 3 d after the damselflies were added. *Epitheca* larvae were used because *Basiaeschna* larvae were not available. Also, four were included because of *Epitheca*'s smaller size. This density of dragonflies is near natural for total dragonfly abundances in fish lakes (McPeek 1990*a*). This experiment was terminated after 45 d.

Food additions in both of these experiments were accomplished by adding large quantities of limnetic zooplankton to cages. Zooplankton were collected from the limnetic zone of Lawrence Lake (Kalamazoo County, Michigan, USA) on mornings when food was to be added. I chose to use limnetic zooplankton from Lawrence Lake for food additions for three reasons: (1) damselfly larvae readily eat limnetic zooplankton species in the laboratory; (2) most of these prey individuals were too large to pass through the mosquito netting; and (3) large quantities of limnetic zooplankton could be collected quickly. All zooplankton collected in three vertical net tows over the entire water column (~12 m depth) with a zooplankton net (30 cm diameter opening, 125-μm mesh size) were added to each food addition cage in both experiments. An equivalent amount of Lawrence Lake water, which had been strained through the zooplankton net to remove zooplankton, was added to each cage that had no food addition as a control for any disturbance or water chemistry effects. Food was added weekly (7, 14, 21, and 28 September, 5 and 12 October) for the duration of both experiments.

Interactions with dragonflies.—These experiments quantified mortality inflicted by coexisting dragonflies and nonlethal effects of the presence of dragonflies (e.g., feeding interference or exploitative competition between the damselflies and their dragonfly predators) on the damselflies.

In the dragonfly lake, 40 *Enallagma boreale* and 15 *I. verticalis* were added to each of the 14 cages in 1995. Three treatments ([1] No Dragonfly, [2] Caged Dragonfly, or [3] Free-Ranging Dragonfly) were then established in these cages. Four replicates each were performed for the No Dragonfly and the Caged Dragonfly treatments, and six replicates were performed for the Free-Ranging Dragonfly treatment. For the Caged Dragonfly treatment, one antepenultimate-instar *Anax junius* larva was placed inside a small enclosure, and the enclosure was placed into the cage. The dragonfly enclosure was 11 × 11 × 6 cm, and was constructed by placing a small, coarse-mesh (openings 1.7 × 1.0 cm), plastic produce container inside a bag constructed of mosquito netting. A glass dowel was placed inside the enclosure for a perch. This enclosure allowed damselflies to detect that a large dragonfly was present by both vision and olfaction, but prevented the dragonfly from eating the damselflies or the damselflies' prey. Identical enclosures without a dragonfly were placed in all other cages. For the Free-Ranging Dragonfly treatment, one unrestrained, antepenultimate-instar *Anax* was placed in the cage. No dragonflies were added to the No Dragonfly treatment cages. This experiment was terminated after 46 d. The cages in this experiment for some unknown reason were significantly contaminated by *Ischnura* moving through the mosquito netting. Consequently, the results for *Ischnura* in this experiment are unreliable and will not be presented.

In the fish lake in 1994, 15 *Ischnura verticalis,* 15 *Enallagma geminatum,* 15 *E. vesperum,* and 5 *E. hageni* were added to each of 14 cages. Four days later one of the three predator treatments described above was assigned to each cage, except that penultimate-instar *Basiaeschna janata* larvae were used instead of *Anax junius.* This experiment was terminated after 46 d.

If dragonflies compete exploitatively with damselflies, damselfly growth should be decreased in the Free-Ranging Predator treatment as compared to the other treatments, because this is the only treatment in which a dragonfly is free to consume prey in the cage. If the presence of dragonflies generates feeding interference in the damselflies (i.e., reduced feeding in the presence of a predator), damselfly growth should also be lower in the Caged Dragonfly treatment as compared to the No Dragonfly treatments. If both exploitation and interference are important, treatment effects should be most pronounced in the Free-Ranging Dragonfly treatment where both exploitation and interference can operate, but treatment effects due to interference should still be detected in the Caged Dragonfly treatment.

Interactions with fish.—This experiment is analogous to the Interactions with Dragonflies experiments, but tests for comparable effects due to fish in the fish lake. In 1994, the same number of damselflies were added to each of 14 cages as follows: 30 *Ischnura verticalis,* 40 *Enallagma geminatum,* 40 *E. vesperum,* and 15 *E. hageni.* This total damselfly density of 125 larvae/cage is somewhat less than the natural density for the cages used (~150 larvae/cage). Five days later one of three predator treatments was constructed in each cage. The three treatments were [1] No Bluegill, [2] Caged Bluegill, or [3] Free-Ranging Bluegill. Four replicates each were performed for the No Bluegill and the Caged Bluegill treatments, and six replicates were performed for the Free-Ranging Bluegill treatment. For the Caged Bluegill treatment, one bluegill (50–65 mm SL) was placed inside a small enclosure, and the enclosure was placed into the cage. The predator enclosures used in this experiment were 25 × 25 × 25 cm, and were constructed of mosquito netting bags around 12 mm diameter PVC (polyvinyl chloride plastic) pipe frames. This again prevented the bluegill from feeding on the damselflies or the damselflies' prey in the cage. Empty containers were placed in cages of the other two treatments. One bluegill of similar size was placed in each of the Free-Ranging Bluegill treatment cages, and no bluegills were added to the No Bluegill treatment cages. This experiment was terminated after 41 d.

RESULTS

Field abundances

The quantitative density estimates obtained in this study are consistent with patterns observed in previous studies (Johnson and Crowley 1980, McPeek 1990*a*). Larval *Enallagma aspersum, E. boreale,* and *E. cyathigerum* were found only in the three dragonfly lakes (Table 2). Five other *Enallagma* species were found only in the three fish lakes (Table 2). A total of thirteen *Enallagma* species inhabit fish lakes of southwestern Michigan (M. A. McPeek, *unpublished data*), but only these five were common enough to be detected by the sampling methods. *Enallagma* species constituted ~85% of the total damselfly assemblage in all six lakes.

Ischnura species were abundant in both lake types (Table 2), and *Ischnura* abundances in the two lake types were similar (t_4 = 0.89, $P > 0.40$ for ln mean abundances in the two lake types).

Laboratory feeding bias

The dragonflies from both lake types and bluegill sunfish all imposed substantially greater mortality on *Ischnura* larvae than on *Enallagma* species with which each predator naturally coexists (Table 3). On average, 65–70% of larvae consumed by both dragonflies were *Ischnura* larvae, and >80% of damselflies consumed by bluegill sunfish were *Ischnura* larvae (Table 3). *Ischnura* larvae were more vulnerable to both dragonflies and fish than were *Enallagma* species that naturally coexist with these predators.

TABLE 2. Larval damselfly density estimates (number of larvae/m^2 lake bottom) from three dragonfly lakes and three fish lakes in southwestern Michigan in a study of the effects of changes in the upper levels of a food web.

	Dragonfly lakes			Fish lakes		
Damselfly species	Turkey Marsh	Marshfield Marsh	Reservoir	Three Lakes II	Palmatier	Hamilton
Enallagma aspersum	0.0 ± 0.0	12.3 ± 27.6	6043.9 ± 1160.9	0.0	0.0	0.0
E. boreale/ cyathigerum	128.5 ± 59.8	166.5 ± 131.9	87.4 ± 36.0	0.0	0.0	0.0
E. antennatum	0.0	0.0	0.0	82.2 ± 57.4	5.1 ± 12.6	10.3 ± 15.9
E. geminatum	0.0	0.0	0.0	82.2 ± 25.2	539.6 ± 329.1	426.6 ± 249.3
E. hageni	0.0	0.0	0.0	195.3 ± 72.1	15.4 ± 25.8	159.3 ± 100.2
E. signatum	0.0	0.0	0.0	215.9 ± 115.4	308.4 ± 428.2	138.8 ± 77.4
E. vesperum	0.0	0.0	0.0	20.6 ± 25.2	66.8 ± 53.1	10.3 ± 25.2
Ischnura posita/ verticalis	15.4 ± 25.8	30.8 ± 37.8	200.4 ± 134.8	5.1 ± 12.6	30.8 ± 47.8	41.1 ± 25.2
Number of samples	6	5	6	6	6	6

Notes: Data are means ± 1 SD. The samples were collected between 26 September 1987 and 9 October 1987.

Field experiments

Intrageneric vs. intergeneric competition.—In these experiments done in both lake types in the absence of predators, significant treatment effects consequent to manipulations in total damselfly density were apparent (some a priori, orthogonal contrasts in the MANOVA of each experiment with $P < 0.05$ for each genus), but these responses were due primarily to differences in growth and not mortality. Manipulations of total damselfly density and generic relative frequency had no consistent effects on the mortality rates of any species in either experiment (all contrasts $P > 0.05$).

In the dragonfly-lake experiment, *Ischnura* growth rates overall were 655% higher than those of *Enallagma boreale* (Fig. 1A, B). Compared to the low total damselfly density, *Ischnura* growth rates were reduced by 12% in the medium total density treatments (contrast testing low vs. medium and high total density treatments: $F_{1,12} = 9.47$, $P < 0.01$) and by 24% in the high total density treatments, although this latter comparison was not statistically significant (contrast testing medium vs. high total density treatments, $F_{1,12} = 3.35$, $P < 0.09$; Fig. 1A). *Ischnura* growth rates did not differ among relative frequency treatments within the medium or high total densities (all contrasts $P > 0.25$; Fig. 1A). *E. boreale* larvae displayed a significant reduction in growth rates only at the high total density treatments (50% reduction in growth rate from the low to high total density treatments; contrast testing medium vs. high total density treatments, $F_{1,12} = 9.69$, $P < 0.01$; Fig. 1B). As with *Ischnura,* relative frequency had no effect on *E. boreale* growth rates when total density was constant (all contrasts $P > 0.05$; Fig. 1B).

The results of the comparable experiment done in the fish lake were similar to those of the dragonfly-lake experiment. In the fish-lake experiment, *Ischnura* growth rates overall were 160% higher than those of *E. geminatum* and 680% higher than *E. vesperum* (Fig. 1C, D). As compared to the low total damselfly density, *Ischnura* growth rates were 20% lower in the high total density treatments, but this difference was only marginally significant (contrast testing medium vs. high

TABLE 3. Results of predator feeding bias experiments for dragonflies and fish from dragonfly and fish lakes.

	Prey			
Predator	*Enallagma* species	*Ischnura* species	*N*†	α_I‡
Dragonfly lakes				
Aeshna mutata	*E. boreale*	*I. verticalis*	12	0.64 ± 0.05*
Fish lakes				
Epitheca cynosura	*E. signatum*	*I. verticalis*	8	0.69 ± 0.06*
Lepomis macrochirus	*E. signatum*	*I. verticalis*	9	0.84 ± 0.10*

* $P < 0.05$ for *t* test of $\alpha_I = 0.50$.

† N = number of replicates of that particular set of species.

‡ Manly's index of preference (α_I) for the predator feeding on *Ischnura* larvae in the trials. Manly's index ranges in value from 0.00 to 1.00; in this experiment α_I is equivalent to the proportion of consumed damselflies that were *Ischnura.* A value of $\alpha_I = 0.50$ in these experiments indicates that the predator displayed no bias in feeding on the two damselfly species. A value of $\alpha_I > 0.50$ indicates that the predator imposed significantly greater mortality on *Ischnura* larvae than on *Enallagma* larvae in the trials. Means ± 1 SE are given with significance noted.

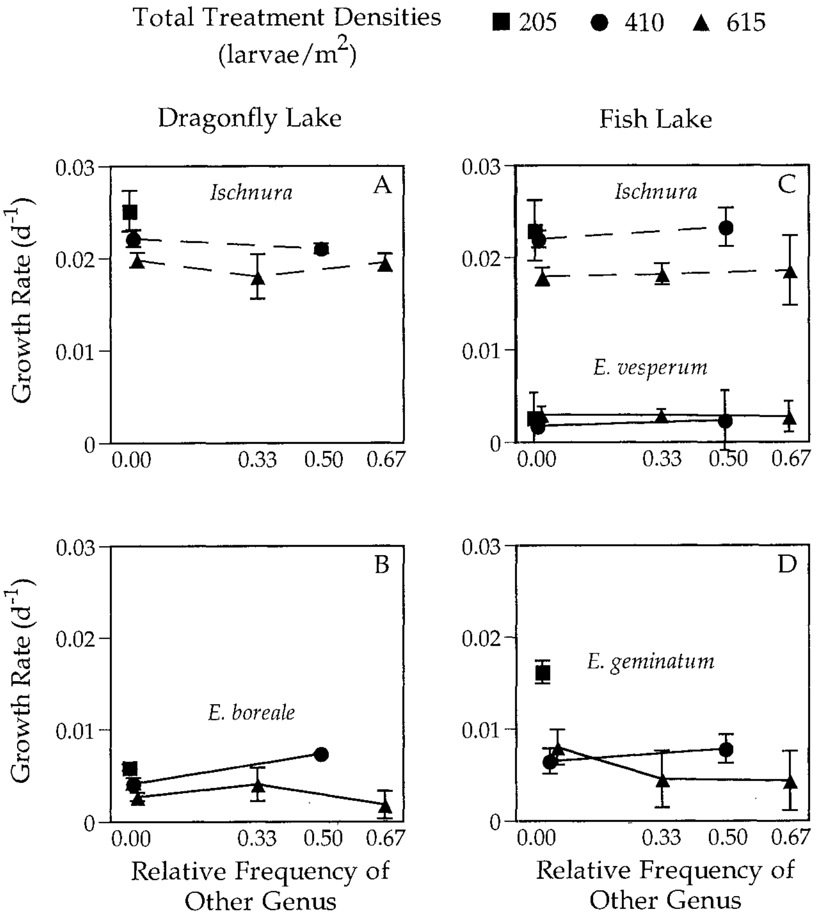

FIG. 1. Growth rates of the damselflies included in the Intrageneric vs. Intergeneric Competition experiments (which were designed to quantify competition among *Enallagma* and *Ischnura* species in the absence of predators) in both lakes. For comparison, the results of the experiment done in the dragonfly lake are given in the left column of panels, and the results of the fish-lake experiment are given in the right-hand column of panels. To permit comparisons between experiments I have given damselfly densities expressed in units of larvae/m^2 of lake bottom. Symbols representing the same total number of damselflies of both genera initially added to cages are connected by lines in the graphs and are given above the panels. The natural density of larvae at the beginning of the experiments was ~685 damselflies/m^2 of lake bottom. The abscissa identifies the relative frequencies of *Ischnura* and *Enallagma* larvae added to cages. Symbols are slightly offset from one another to aid in interpretation. Each species is only present in six of the nine treatments (Table 1).

total density treatments, $F_{1,12} = 4.33$, $P < 0.06$; Fig. 1C), but *Ischnura* growth rates did not differ among the various treatments at the low or medium total densities (all contrasts $P > 0.20$) or among the relative frequency treatments within the high total density (all contrasts $P > 0.85$). *E. vesperum* growth rates were unaffected by all density and relative frequency treatments (all contrasts $P > 0.60$; Fig 1C). *E. geminatum* larvae had a 160% higher growth rate when at low density in the absence of *Ischnura* as compared to the other treatments (contrast testing low vs. medium and high total density treatments, $F_{1,12} = 16.86$, $P < 0.001$), but *E. geminatum* growth rates did not differ among any of the other treatments (other contrasts $P > 0.20$; Fig. 1D).

In both lake types, damselflies clearly compete with one another, because increasing total damselfly density causes decreases in their growth rates. However, *Ischnura* and *Enallagma* species appear to be relatively equivalent competitors, since the relative abundances of the two genera do not affect growth rates.

Density manipulation in the presence of dragonflies.—In the experiment done in the dragonfly lake, *Anax* dragonfly larvae were not recovered from two cages in the high total damselfly density treatment; these individuals apparently died sometime during the experiment. These two cages were therefore excluded from analyses.

In the dragonfly-lake experiment, I was unable to perform an overall MANOVA because the loss of the two cages reduced the total degrees of freedom. However, univariate analyses indicate that increasing total damselfly densities had no effect on *Enallagma boreale* or *Ischnura* mortality rates (overall treatment effects for both species $P > 0.30$; Fig. 2A) or on their growth rates (overall treatment effects for both species $P >$

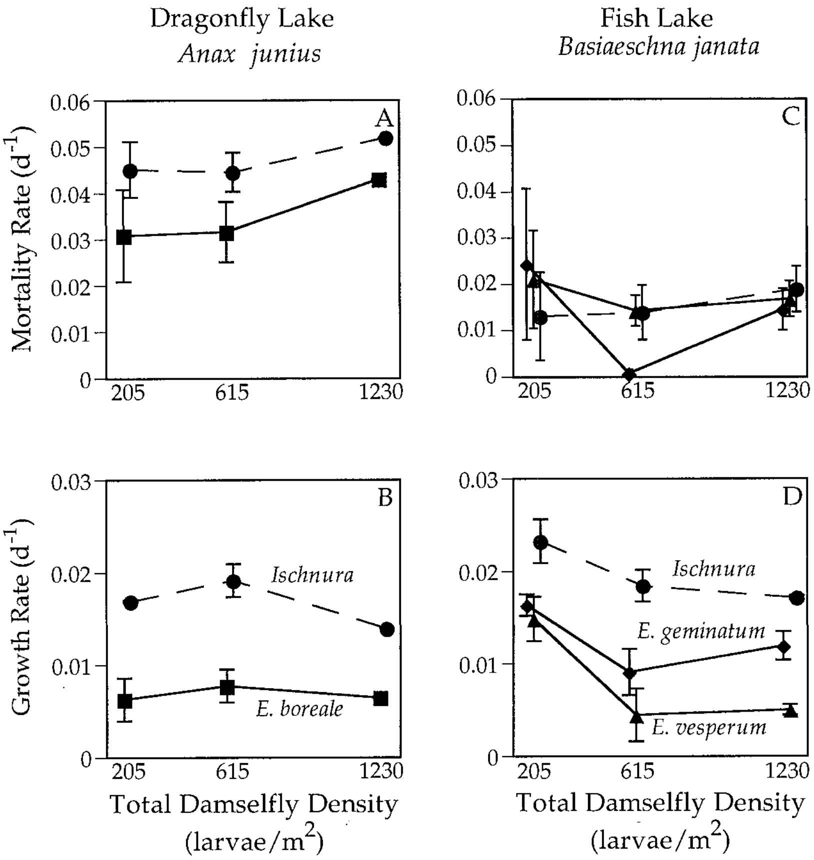

FIG. 2. Rates of mortality and growth for the damselfly species included in the Density Manipulation in the Presence of Dragonflies experiments done in each lake. The species of dragonfly used in each experiment is given above the column of panels. The abscissa gives the total number of damselflies initially added to cages. The natural density of larvae at the beginning of the experiments was ~685 damselflies/m^2 of lake bottom. Symbols are the means ± 1 SE for each species in a treatment. Symbols are slightly offset from one another to aid in interpretation.

0.10; Fig. 2B). I also calculated Manly's preference index (α_I) for the number of larvae of each species recovered from each cage to test explicitly for a difference in mortality rate between the two genera. Averaged across all density treatments, Manly's index for *Ischnura* was $\alpha_I = 0.62 \pm 0.08$ (mean ± 1 SE), which is not statistically significantly different from no preference ($t_6 = 1.47$, $P = 0.10$) but is, however, nearly identical to the value measured in the laboratory feeding bias experiment with *Aeshna mutata* (Table 3).

In the experiment done in the fish lake, the contrast testing the low vs. medium and high total damselfly density treatments in the MANOVA was not statistically significant ($F_{6,1} = 16.19$, $P = 0.095$). This overall test was not statistically significant because it includes both mortality and growth rates for all three species as response variables. Univariate ANOVAs indicate that mortality rates of all three species were not different among the three total damselfly density treatments (all contrasts $P > 0.30$; Fig. 2C). However, all three species had depressed growth rates at the medium and high total damselfly density as compared to the low density (Fig. 2D): *Ischnura* growth rates were depressed by 30% ($F_{1,6} = 6.94$, $P < 0.05$), *E. vesperum* growth rates by 70% ($F_{1,6} = 14.39$, $P < 0.01$), and *E. geminatum* growth rates by 35% ($F_{1,6} = 6.78$, $P < 0.05$). Growth rates did not differ between the medium and high total density treatments for any species (all $P > 0.40$).

Dragonflies do not impose density-dependent mortality on coexisting damselflies in either lake type. Also, competitive effects among damselflies in the presence of foraging dragonflies are only apparent in fish lakes.

Density manipulation in the presence of fish.—In 1995 an unusually late hatch of *E. geminatum* caused substantial contamination by many small larvae of this species into cages of this experiment. Therefore, results for *E. geminatum* will not be reported.

In this experiment done in the fish lake, the mortality and growth of both *Ischnura* and *E. vesperum* changed with damselfly density in the presence of bluegill sunfish. The design of the experiment did not permit an overall MANOVA test including the mortality and growth rates of both species simultaneously, but separate MANOVAs for each species were done. The combined mortality and growth rate responses of *Ischnura*

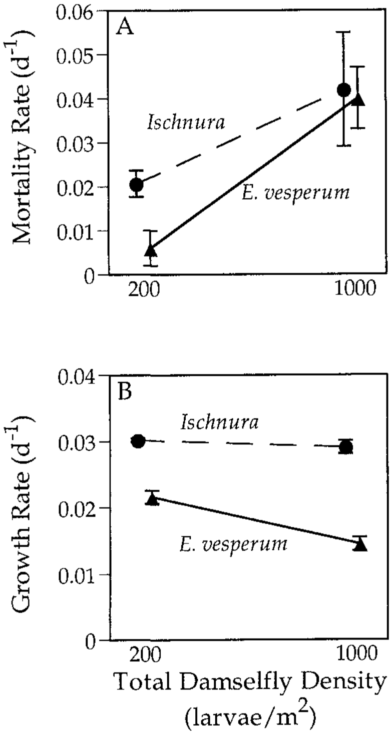

FIG. 3. Rates of mortality (A) and growth (B) for *Ischnura* and *E. vesperum* in the Density Manipulation in the Presence of Fish experiment done in a fish lake. The abscissa gives the total number of damselflies initially added to cages. The natural density of larvae at the beginning of the experiment was ~685 damselflies/m^2 of lake bottom. Symbols are the means ± 1 SE for each species in a treatment. Symbols are slightly offset from one another to aid in interpretation.

between the two total damselfly density treatments were significant in the overall MANOVA ($F_{2,3} = 35.98$, $P < 0.03$), with mortality rate increasing and growth rate decreasing with increasing total damselfly density (Fig. 3). Likewise, *E. vesperum* mortality rate increased and growth rate decreased with increasing total damselfly density ($F_{2,3} = 15.42$, $P < 0.03$; Fig. 3).

To test whether death rates of *Ischnura* were higher than those of *E. vesperum,* I also calculated Manly's index (α_I) for *Ischnura. Ischnura* experienced higher mortality rates than *E. vesperum* from fish predation in the low density cages ($\alpha_I = 0.80 \pm 0.15$ (mean ± 1 SE)), but this was not significantly different from no bias in mortality rates ($t_2 = 2.04$, $P > 0.25$) because of low statistical power (i.e., df = 2). However, this value for Manly's index is very similar to the value obtained in the laboratory experiments for bluegill sunfish (Table 3). Fish displayed no feeding bias in the high density treatment ($\alpha_I = 0.50 \pm 0.03$, $t_2 = 0.13$, $P > 0.90$).

Fish impose higher per capita mortality rates on coexisting damselflies as total damselfly density increases. Also, the effects of competition among the damselflies (i.e., decreased growth rates) are evident in the presence of foraging fish predators.

Food addition.—For the food addition experiment performed in the dragonfly lake, the overall MANOVA results including the mortality and growth rates of both species showed no effect of the food addition treatment (food addition main effect $F_{4,8} = 0.91$, $P > 0.50$) but showed a significant density effect ($F_{4,8} = 5.82$, $P < 0.02$). The interaction between density and food addition was not significant ($F_{4,8} = 0.08$, $P > 0.98$). For both *Enallagma boreale* and *Ischnura,* mortality rates increased and growth rates decreased with increasing total damselfly density (Figs. 4A, B).

In contrast, in the fish lake the addition of food increased growth rates for both *Enallagma vesperum* and *Ischnura,* and lowered mortality rates for *Ischnura* (MANOVA food addition main effect: $F_{6,7} = 3.94$, $P < 0.05$) (Fig. 4C, D). Also, for both species growth rates were higher and mortality rates lower in the low damselfly density treatment as compared to the high damselfly density treatments with or without dragonflies (MANOVA density/dragonfly main effect: $F_{12,14} = 8.78$, $P < 0.0001$) (Fig. 4C, D). The interaction between the density/dragonfly and food addition treatments was not significant ($F_{12,14} = 1.82$, $P > 0.14$).

Competition among damselflies in dragonfly lakes must occur via interference, because they are not food limited. In contrast, damselflies in fish lakes are food limited, indicating that competition for resources influences damselfly growth and mortality rates in fish lakes.

Interactions with dragonflies.—Contamination of cages by *Ischnura* larvae during the experiment made the interpretation of results for *Ischnura* impossible for the experiment done in the dragonfly lake. Therefore, results for only *Enallagma boreale* are presented. Mortality rates were significantly higher and growth rates were significantly lower for *E. boreale* when *Anax* larvae were free to forage in cages as compared to the No Dragonfly or Caged Dragonfly treatments (MANOVA contrast: $F_{2,10} = 31.22$, $P < 0.0001$) (Fig. 5A, B). *E. boreale* mortality rates in the presence of free-ranging *Anax* larvae in cages were very similar to natural mortality rates in local dragonfly lakes (0.027 ± 0.007 d^{-1} [mean ± 1 SE]; McPeek 1990*a*).

The apparent decrease in *E. boreale* growth rate when *Anax* was free to forage could have been the result of positive size-selective predation by the predator in the Free-Ranging Dragonfly treatment and not a real decrease in growth rate. If larvae are growing at slower rates, they should also have less mass when standardized to a given head width (Johnson et al. 1984, Pierce et al. 1985). To test this, I performed an analysis of covariance of ln(dry mass) with ln(head width) as a covariate, including all larvae recovered from cages in the three treatments in the analysis. The slopes of the regressions of ln(dry mass) on ln(head width) did not differ among the three treatments ($F_{2,299} = 0.04$, $P >$

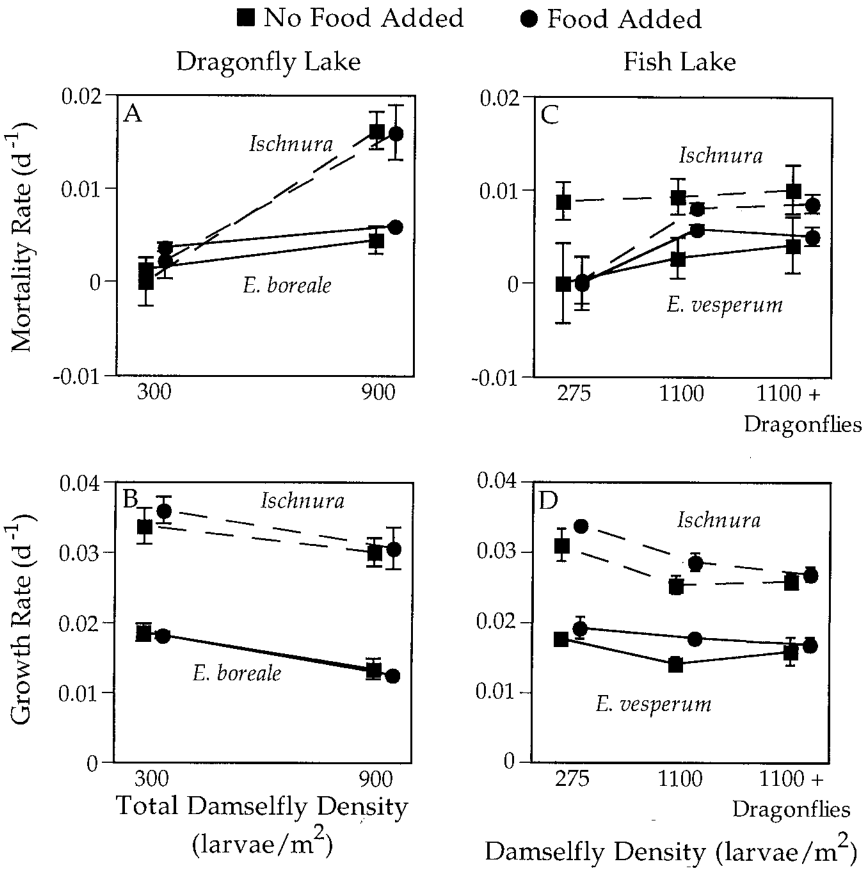

FIG. 4. Rates of mortality and growth for the indicated damselfly species with or without added food, in each lake. For the dragonfly-lake experiment, the mortality rates (A) and growth rates (B) for *Ischnura* (– – –) and *E. boreale* (———) are given. For the fish-lake experiment, the mortality rates (C) and growth rates (D) for *Ischnura* (– – –) and *E. vesperum* (———) are given. The abscissa gives the damselfly density levels; larvae of predaceous dragonflies (*Epitheca*) were added in the fish lake only to damselfly treatments with highest density, as shown. Symbols for the food addition treatment are identified above the panels. The natural density of larvae at the beginning of the experiments was ~685 damselflies/m^2 of lake bottom. Symbols are the means ± 1 SE for each species in a treatment. Symbols are slightly offset from one another to aid in interpretation.

0.95), but the intercepts of the lines for the three treatments differed significantly from one another. The intercept of the Free-Ranging Dragonfly treatment was significantly below the intercepts for the other two ($F_{1,301} = 10.93$, $P < 0.002$), and the intercept for the Caged Predator treatment was below the intercept for the No Predator treatment ($F_{1,301} = 7.89$, $P < 0.006$). This result does not preclude a contribution of size-biased foraging, but it does show that *E. boreale* growth rates were lower when *Anax* dragonflies were present and particularly when they were free to forage in cages.

In the experiment done in the fish lake, the dragonfly treatments had no substantial effects on the general patterns of growth or mortality rates among the four damselfly species (MANOVA overall treatment effects: $F_{16,8} = 1.45$, $P > 0.30$) (Figs. 5C, D). Inspection of the univariate analyses indicates that the only responses consistent with expectations were a decrease in *Ischnura* growth rate in the two treatments in which *Basiaeschna* dragonflies were present ($F_{1,11} = 4.98$, $P <$ 0.05) and a decrease in *E. geminatum* growth rate when dragonflies were free to forage in cages ($F_{1,11} = 18.83$, $P < 0.002$) (Fig. 5D).

Large dragonflies in dragonfly lakes impose substantial mortality on coexisting damselflies, and also cause a reduction in damselfly growth rates. In contrast, the dragonflies found in fish lakes do not significantly increase the mortality of coexisting damselflies, and have variable effects on damselfly growth.

Interactions with fish.—Bluegills in three cages died during the course of this experiment; two in the Free-Ranging Bluegill treatment and one in the Caged Bluegill treatment have therefore been excluded from analyses. Consequently, I was unable to perform a MANOVA including the mortality and growth rates of all four damselfly species in one analysis. Instead, I performed separate MANOVA analyses of species mortality rates and of species growth rates.

Mortality rates of all species increased substantially when bluegill were free to forage in cages as compared

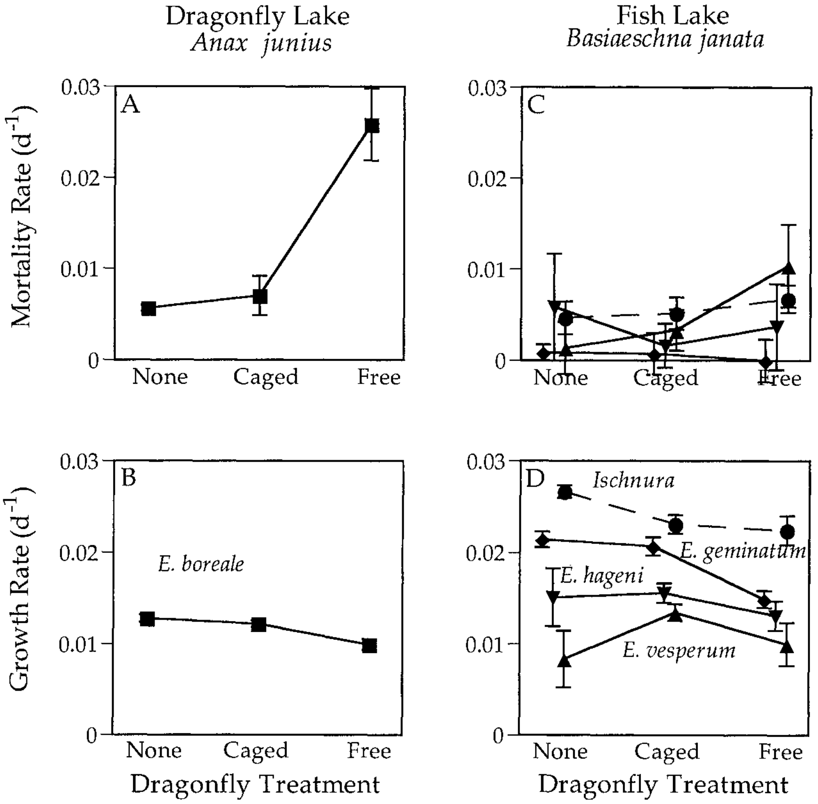

FIG. 5. Rates of mortality and growth for the damselfly species included in the Interactions with Dragonflies experiments done in each lake. For the dragonfly-lake experiment, the mortality rates (A) and growth rates (B) for *E. boreale* (—■—) are given. For the fish-lake experiment, the mortality rates (C) and growth rates (D) for *Ischnura* (—●—), *E. geminatum* (—♦—), *E. hageni* (—▼—), and *E. vesperum* (—▲—) are given. The species of dragonfly used in each experiment is given above the column of panels. The abscissa gives the dragonfly treatments applied to cages. All cages were started with 750 total damselflies/m^2 (~685 damselflies/m^2 of lake bottom is natural at that time of year). Symbols are the means ± 1 SE for each species in each treatment. Symbols are slightly offset from one another to aid in interpretation.

to the other two treatments (MANOVA contrast: $F_{4,5} = 33.38$, $P < 0.0008$), but mortality rates did not differ between the No Bluegill and Caged Bluegill treatments (MANOVA contrast: $F_{4,5} = 2.08$, $P > 0.22$) (Fig. 6A). Damselfly growth rates were unaffected by the predator treatments in this experiment (MANOVA overall treatment effects: $F_{4,5} = 0.41$, $P > 0.88$).

Fish, as exemplified by bluegills here, impose substantial mortality on coexisting damselflies, but their presence does not appear to affect damselfly growth rates.

DISCUSSION

Previous work has shown that the alternative lake types examined in this study are the natural littoral systems that develop when fish are consistently present or absent from a permanent water body in this region of North America (Crowder and Cooper 1982, McPeek 1990*a*, Werner and McPeek 1994). The experiments performed in this study were designed to elucidate the mechanisms and strengths of interactions affecting larval damselfly mortality and growth in each system. The experimental designs also allow comparisons between results from manipulating similar food web components in the two lake types. Comparing food web interactions that affect damselflies in dragonfly and fish lakes explore the consequences of changing the top predator in this system.

The first striking feature of this comparison is the difference in species assemblages between dragonfly and fish lakes. Many littoral taxa have some species that are unique to each of the dragonfly and fish lake types, and other species that maintain populations in both systems (Hendrikson and Oscarson 1978, 1981, Collins and Wilbur 1979, Eriksson et al. 1980, Kerfoot 1982, Cook and Streams 1984, Brown and DeVries 1985, Bendell 1986, McPeek 1989, Werner and McPeek 1994). Such differences in species composition are also evident in the limnetic zones of these same water bodies (Brooks and Dodson 1965, Sprules 1972, Dodson 1970, 1974, von Ende 1979, Zaret 1980, Vanni 1986, 1988, Arnott and Vanni 1993). In the odonates, *Enallagma* species segregate between the two lake types, and large, active dragonfly species, which are top predators in fishless waters, are replaced by smaller, less active species in fish lakes (Benke 1978, Johnson and Crowley 1980, Morin 1984*a*, *b*, Crowley et al.

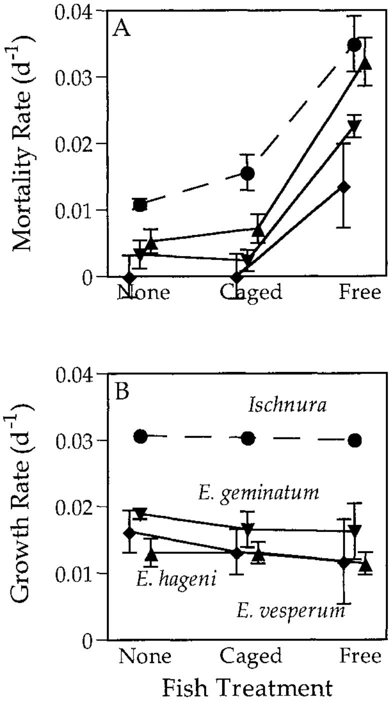

FIG. 6. Rates of mortality (A) and growth (B) for *Ischnura* (—●—), *E. geminatum* (—♦—), *E. hageni* (—▼—), and *E. vesperum* (—▲—) in the Interactions with Fish experiment done in the fish lake. The abscissa gives the fish treatments applied to cages. All cages were started with 560 total damselflies/m^2 (~685 damselflies/m^2 of lake bottom is natural at that time of year). Symbols are the means ± 1 SE for each species in a treatment. Symbols are slightly offset from one another to aid in interpretation.

1987, Pierce 1988, McPeek 1990*a*, Wissinger 1992). However, wholesale species replacement does not occur; the same *Ischnura* species are common to both lake types, as are a third group of dragonfly species (Table 2; see also Johnson and Crowley 1980, McPeek 1990*a*). Little is known about the species-level changes in taxa that dominate the diets of damselflies (e.g., chironomids, oligochaetes, littoral crustaceans). However, if there are compositional changes in taxa that are resources for damselflies, these changes apparently do not cause substantial differences in damselfly growth rates between the two lake types (e.g., compare *Ischnura* growth rates in experiments between the lake types).

The second striking feature of the comparison of food webs in dragonfly and fish lakes is the alteration in strengths and mechanisms of interactions among these taxa. Models encapsulating food web organization into discrete trophic levels (e.g., Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981, Carpenter and Kitchell 1993) would predict that adding fish to a previously fishless system should (1) cause a change in the mechanisms regulating dragonfly populations from competition in dragonfly lakes to fish predation in fish lakes, and (2) consequently cause a shift in the mechanisms regulating damselfly abundances from primarily predator limitation in dragonfly lakes to resource limitation in fish lakes. Alternatively, models recognizing that the trophic positions of species are not always clearly hierarchical (e.g., Menge and Sutherland 1976, 1987) would predict that damselfly abundances should be influenced more by predation and less by resource competition in fish lakes because more species are above them in the food web. The general patterns of interaction strengths affecting damselfly mortality and growth in the two lake types are superficially consistent with some features of these general models of community organization, but in most cases for the wrong reasons.

Overall, natural damselfly mortality rates in fish lakes are about one-third of those in dragonfly lakes (McPeek 1990*a*), and damselflies compete for resources in fish lakes but not in dragonfly lakes (Fig. 4). Also, dragonflies in dragonfly lakes are regulated in the larval phase by strong competitive interactions with one another (Van Buskirk 1988, 1989, 1992, 1993, Wissinger 1989, 1992, Wissinger and McGrady 1993), and they impose substantial mortality on coexisting damselflies, accounting for >75% of total damselfly mortality (Fig. 5; McPeek 1990*a*). In contrast, dragonflies in fish lakes suffer substantial losses to fish predation (Morin 1984*a*, *b*, Pierce 1988, Johnson et al. 1995), and interactions among dragonflies are relatively weak (Crowley et al. 1987, Johnson et al. 1987, but see Benke 1978), but dragonflies did not impose detectable mortality on coexisting damselflies (Fig. 5).

These results would seem to support the models descended from Hairston et al. (1960). However, the food webs of the two lake types differ in ways not predicted by these models. Instead of fish on the top trophic level regulating dragonfly abundances in the next lower trophic level and thereby allowing damselfly abundances at the second lower trophic level to increase to levels where they compete for resources, fish are the primary mortality agent for damselflies in fish lakes (Fig. 6; McPeek 1990*a*). Dragonflies in fish lakes are in essence demoted to the same trophic level as damselflies; the dragonfly–damselfly interaction shifts from predator–prey in dragonfly lakes to weak competition in fish lakes (cf. Figs. 2 and 5). Also, this shift in interaction mechanism among dragonflies and damselflies is not the result of changes in dragonfly abundances as these models hypothesize; dragonflies are generally as abundant or more abundant in fish lakes than in dragonfly lakes (Johnson and Crowley 1980, McPeek 1990*a*). Rather, the change in mechanism is due to the replacement of large, active dragonflies in dragonfly lakes (Ross 1971, Folsom and Collins 1984, Bergelson 1985, Wissinger 1992) by smaller, sit-and-wait dragonflies in fish lakes (Crowley and Johnson 1982, Morin 1984*a*, *b*, Crowley et al. 1987, Pierce 1988). Alternatively, as in the Menge and Sutherland (1976, 1987) models, more potential predators exist in fish lakes, but resource competition becomes important when fish are added to the system, which is contrary to the predictions of these models. Change in the abilities of species at various food web positions to engage in different types of species interactions, because of change in species composition, is the primary cause of change in the mechanisms and strengths of species interactions, not simply change in the abundances of species or whole trophic levels.

The role that fish play in this system also does not fit the classic notion of a keystone predator that preferentially consumes a competitive dominant (e.g., Paine 1966, 1974, Menge et al. 1994). Instead of reducing the abundances of superior competitors, fish predation excludes an alternative set of predators (i.e., large dragonflies) from lakes with fish (Hall et al. 1970, Crowder and Cooper 1982, Hambright et al. 1986, Werner and McPeek 1994; see also Thorp 1986). Damselfly assemblage compositions in fish and dragonfly lakes are set primarily by the abilities of species to deal with alternative predation regimes (McPeek 1990*a*, *b*, 1995, McPeek et al. 1996). For example, *Enallagma vesperum* transplanted to a dragonfly lake experienced mortality rates of $0.107 \pm 0.006\ \text{d}^{-1}$ with *Anax* dragonflies, and *Enallagma boreale* transplanted into a fish lake experienced mortality rates of $0.056 = 0.008\ \text{d}^{-1}$ with bluegill (McPeek 1990*a*). These mortality rates of transplants are higher than mortality rates of any native species measured in this and previous studies (McPeek 1990*a*). Similar contrasts can be made for the limnetic zones of these lakes where differences in zooplankton assemblages are primarily caused by differential vulnerabilities to fish and other large invertebrate predators (e.g., *Chaoborus* and *Notonecta* species) (von Ende 1979, Vanni 1988, Arnott and Vanni 1993).

Food web interactions in the two lake types

The structure of the food web within each lake type is consistent with "keystone predation" models of predation promoting coexistence between competing prey (Levin 1970, Phillips 1974, Vance 1978, Leibold 1989, 1996, Holt et al. 1994). These models predict that coexistence of species with shared predators and resources is more likely if trade-offs cause some species to be more successful at avoiding predation and other species to be more successful at utilizing resources. Such trade-offs promoting coexistence have been identified in other natural systems. For example, coexistence of some desert rodents is enabled by species differentially utilizing microhabitats that provide either high foraging returns along with high predation rates or low foraging returns along with low predation rates (Price and Brown 1983, Kotler 1984, Kotler and Brown 1988, Brown 1989, Kotler et al. 1991, Longland and Price 1991). Similar partitioning between areas of low predation risk/low foraging return and high predation risk/high foraging return appears to promote coexistence in zooplankton (Leibold 1991, Tessier and Welser 1991) and fish assemblages (Werner and Hall 1977). *Ischnura* and *Enallagma* species do not partition space as in these other systems, but rather are simultaneously exposed to the same predators and resources (Johnson and Crowley 1980, McPeek 1990*a*). However, comparison of food web interactions affecting the damselflies indicates that coexistence of *Enallagma* and *Ischnura* species in each lake type is fostered by analogous trade-offs.

Competitive interactions among the damselflies in the absence and presence of predators were phenomenologically similar in the two lake types, but different mechanisms of competition operate. This and other studies have shown that damselfly growth rates in the absence of predators in both lake types are higher when total densities are <275 larvae/m^2 (Johnson et al. 1984, Pierce et al. 1985, McPeek 1990*a*), and the relative frequency of the two genera has no effect on their growth rates (Fig. 1). In the laboratory, damselflies of both genera reduce their feeding activities in the presence of dragonflies, fish, and other damselflies (Heads 1985, Pierce et al. 1985, McPeek and Crowley 1987, Dixon and Baker 1987, 1988, Jeffries 1990, McPeek 1990*b*, Johansson 1993, Richardson and Anholt 1995). Damselflies are not food limited in dragonfly lakes (Fig. 4), implying that competitive interactions among damselflies and reduced growth responses in the presence of dragonflies must be due exclusively to reduced feeding activity (i.e., feeding interference). However, in fish lakes, damselflies are food limited (Fig. 4), indicating that reduced growth responses in that lake type are probably due to a combination of competition for resources and feeding interference.

Ischnura growth rates were also consistently higher across all experiments in both lake types and relatively less affected by increased competition than those of *Enallagma* species. The lack of response for any species to changes in relative frequency of the two genera in the Intrageneric vs. Intergeneric Competition experiments suggests that *Ischnura* and *Enallagma* species are similar interference and resource competitors. The difference in growth rates between the genera must therefore be some combination of (1) differential abilities to procure prey at a given resource level, (2) differential abilities to convert captured food into their own biomass, or (3) differences in the levels of behavioral responses generating feeding interference. From a theoretical perspective, this means that the genera differ not in their effects on resource abundances, but rather in their responses to resource abundances (sensu Goldberg 1990, Leibold 1995). These results suggest that either *Ischnura* foraging rates at a given resource level are higher, or their assimilation rates and/or efficiencies are higher than those of *Enallagma.* In studies of the European *Ischnura elegans,* assimilation rate is strongly correlated with larval growth rate (Lawton et al. 1980). However, studies that would allow comparisons of relevant foraging and digestive physiological parameters for *Enallagma* and *Ischnura* have not been performed. Such studies would provide valuable insights into the mechanisms affording *Ischnura* the substantial growth advantage over *Enallagma*.

Dragonfly predation accounts for >75% of larval damselfly mortality in dragonfly lakes. Mortality rates of *E. boreale* quadrupled when dragonflies were free to forage (Fig. 5A); similar increases in *Enallagma* mortality rates due to dragonfly predation have been observed in other experiments (McPeek 1990*a*, Wissinger and McGrady 1993). Although similar comparisons within the same experiment cannot be made for *Ischnura,* the consistency of damselfly death rates between experiments, between sites, and between years for similar experimental conditions (McPeek 1990*a*) suggests that cross-experimental comparisons are justified. Comparing mortality rates for *Ischnura* between the Density Manipulation in the Presence of Dragonflies experiment (Fig. 2A) and the High Density treatment of the Food Addition experiment, in which no large dragonflies were present, shows that *Ischnura* mortality rates increase by a factor of 2.5 when these damselflies are exposed to dragonfly predation. Also, given that *E. boreale* mortality rates in natural populations are very similar to those in the presence of dragonflies in these and previous experiments, the greater mortality rates for *Ischnura* as compared to *E. boreale* probably accurately reflect *Ischnura*'s greater relative susceptibility to dragonfly predators in dragonfly lakes (Table 3, Fig. 2A).

Given that initial densities in the dragonfly-lake Interactions with Dragonflies experiment were the same as the highest total damselfly density used in the Intrageneric vs. Intergeneric Competition experiment, and growth rates were lower in the presence of dragonflies (Fig. 5B), feeding interference generated by the presence of large dragonflies must be greater than feeding interference due to high damselfly densities. This can explain why no growth effects were observed across a damselfly density gradient when dragonflies were present (Fig. 2B); the presence of the dragonfly depressed damselfly growth rates below what they would have been with only interference among the damselflies at each density. This result implies that the depression of growth rates via feeding interference from the presence of various species is hierarchical and non-additive (see also Wissinger and McGrady 1993). Increased damselfly densities impose some level of threat to damselflies and their growth rates are depressed because of increased time interacting with other damselflies (McPeek and Crowley 1987). However, in the presence of threatening predators, feeding reductions, because of greater predator vigilance and decreased activity to avoid detection by predators (McPeek 1990*b*), have a substantially greater depressive effect on growth rates regardless of damselfly density. Dragonflies have an overriding impact on damselfly growth as well as mortality in the dragonfly-lake system (see also Kohler and McPeek 1989, Fraser and Gilliam 1992, Culp and Scrimgeour 1993, Peckarsky et al. 1993, Scrimgeour and Culp 1994, Werner and Anholt 1996 for other examples of lethal vs. nonlethal effects of predators).

Clearly, interactions between dragonflies and damselflies in dragonfly lakes are quite strong, but whether predation by dragonflies contributes to the regulation of damselfly populations is still unclear. Damselfly mortality rates do not increase as damselfly densities increased in the presence of dragonflies (Fig. 2A), and so dragonflies do not impose direct negative density dependence that would regulate damselfly abundances. However, reduced growth rates due to feeding interference could increase the total mortality experienced by a cohort of larvae by increasing the duration of the larval period and thus the amount of time larvae are exposed to dragonfly predation. I am currently developing demographic models to explore whether the reductions in growth rate identified in these experiments are sufficient to generate negative density dependence in total larval mortality. To test these models, experiments that span the entire larval phase of the life cycle from hatching to metamorphosis (and multiple generations if possible) will be required.

In fish lakes, fish are a primary mortality source. Mortality rates of all damselflies increased when bluegills were permitted to forage in cages (Fig. 6; see also McPeek 1990*a*, Blois-Heulin et al. 1990), and mortality rates increased with damselfly density in the presence of bluegills (Fig. 3). Also, *Ischnura* experience greater mortality from fish than do *Enallagma* larvae. In the laboratory, *Ischnura* were eaten at greater rates by bluegills than *E. vesperum.* In the field, *Ischnura* had higher mortality rates than *E. vesperum* in the presence of bluegills in both experiments, but especially at lower damselfly densities (Figs. 3A and 6A), and *Ischnura* had substantially higher death rates than the other two *Enallagma* species (Fig. 6A). Fish predation is an important regulatory force generating negative density-dependent mortality in both genera, with *Ischnura* being relatively more susceptible than coexisting *Enallagma* species.

In contrast to fish, both *Basiaeschna* and *Epitheca* dragonflies in fish lakes imposed no detectable mortality on damselflies in any of the three field experiments in which they were included (Figs. 2C, 4C, and 5C). This was surprising, since previous studies have found that these dragonflies can inflict significant mortality on odonates when large size differences exist between individuals (Benke 1978, Benke et al. 1982, Morin 1984*a*, *b*, Johnson et al. 1985, Crowley et al. 1987). *Basiaeschna* and *Epitheca* individuals used in these experiments began as penultimate instars, whereas the damselflies began experiments as small instars, so the size differences between dragonflies and damselflies were always initially large in experiments.

Results of these experiments do, however, indicate that dragonflies and damselflies are competitors in fish lakes. These dragonflies have been shown to depress the standing crop of invertebrates that are staples in damselfly diets, e.g., oligochaetes, crustaceans, chironomids (Thorp and Cothran 1984, Johnson et al. 1987). In this study, the decrease in *Ischnura* growth rates across treatments was consistent with feeding interference in the Interactions with Dragonflies experiment, but the *Enallagma vesperum* treatment responses were consistent with resource competition (Fig. 5D). With food supplementation both *Ischnura* and *E. vesperum* grew less at high densities when dragonflies were present as compared to the high density treatment in the absence of dragonflies (Fig. 4D). Given that damselfly growth rates were lower as their density increased in the presence of dragonflies (Fig. 2D), resource competition between damselflies and dragonflies must have contributed to the growth responses in the Food Addition experiment (remember that the effect of interference with dragonflies in the dragonfly lake was independent of damselfly density [Fig. 2B]). These results suggest that both exploitative and interference mechanisms contribute to determining the competitive effects of dragonflies on damselflies.

The higher growth rates of *Ischnura* may also ameliorate the impacts of predation in both lake types. In Michigan where these experiments were conducted, *Ischnura* and *Enallagma* species are univoltine (M. A. McPeek, *personal observation*). *Ischnura* eggs hatch much later in the summer than *Enallagma* (M. A. McPeek, *personal observation*), and *Ischnura* species are the first damselflies to metamorphose into adults in the spring (M. A. McPeek, *unpublished data*; see also Walker 1953, Carpenter 1991, Barber 1993). By hatching from eggs later in the summer and emerging from the water earlier in the spring, *Ischnura* species have a substantially shorter larval period and are thus exposed to dragonflies and fish for shorter time periods as compared to *Enallagma* species. Faster growth rates permit this shortening of the larval period.

Overall, these results are consistent with "keystone predation" models predicting that coexistence is fostered when some species are better at avoiding predators and other species are better at utilizing resources (Levin 1970, Phillips 1974, Vance 1978, Leibold 1989, 1996, Holt et al. 1994). In each lake type, *Ischnura* utilize resources more effectively than native *Enallagma,* but native *Enallagma* avoid predators more effectively than *Ischnura.* Obviously, the food webs in these natural systems are more complex than these simple models. For example, bluegill feed in the littoral zones of lakes only when small; larger size classes feed on zooplankton in the limnetic zones (Werner and Hall 1977, 1988). As a consequence, littoral prey abundances only influence the survival of small bluegill (Mittelbach and Osenberg 1993). Clearly, both predation and competition contribute to regulating the abundances of species in both damselfly genera in fish lakes, and as a result the genera's abundances are dynamically linked via indirect effects propagated through both resources and predators. However, more complicated models and experiments are required to evaluate how age or size structure in the top predator influences the conditions for coexistence of mid-level consumers like the damselflies.

Enallagma and *Ischnura* also differ as predicted by these models in dragonfly lakes, but this difference may not be absolutely critical to their coexistence in this lake type. Dragonfly predation is not density dependent. Also, any "apparent" competitive interactions (sensu Holt 1977) between the genera mediated through dragonfly populations are probably weak. Adults of many of the large dragonfly species that are restricted to fishless lakes as larvae migrate great distances in the spring and fall (Trottier 1966, 1971, May 1992). Consequently, immigration and emigration rates may substantially determine the abundances of dragonfly larvae in any particular dragonfly lake, and not demographic responses to local prey availability. Also, these dragonflies display a substantial degree of feeding interference effects on their own densities (Van Buskirk 1988, 1989, 1992, 1993, Wissinger 1989), which will also diminish any apparent competitive effects mediated through dragonfly abundances. Since the damselflies do not compete for resources and interference competition is symmetrical between them, any indirect interactions between the genera mediated through predators or resources should also be effectively decoupled. Therefore, trading off the abilities to avoid predators and utilize resources may promote their coexistence in dragonfly lakes but may not be absolutely critical; coexistence may be possible simply because each can maintain populations in this lake type.

Differential responses to changing the top predator

The structures of the food webs surrounding the damselflies imply that trade-offs operating on different spatial and temporal scales simultaneously influence the distributions and abundances of species in this system (McPeek 1996*a*). Within each lake type, a trade-off in predator avoidance and resource utilization abilities promote coexistence of the genera (and may be critical to their coexistence in fish lakes). However, the differences in food web interactions associated with having different top predators create another trade-off between the lake types for *Enallagma* but not for *Ischnura,* and this difference for the two genera results specifically from their respective positions within each food web. Because *Enallagma* are better adapted to avoiding predators within each lake type (i.e., their food web position within each lake type), they also face a trade-off between the two lake types in the specificity of their antipredator abilities. As a result, *Enallagma* species segregate between lake types; species in each lake type have evolved antipredator defenses that are successful against the predator with which they live but that come at the expense of defenses against the other predator as well as resource utilization abilities (Pierce et al. 1985, McPeek 1990*b*, 1995, McPeek et al. 1996). In contrast, because *Ischnura* are better adapted to utilizing resources (i.e., their food web position within each lake type), they do *not* face a trade-off between these two food webs; their abilities to utilize resources are critical to their persistence in both lake types, and substituting a different top predator does not directly affect resources. Consequently, *Ischnura* are able to inhabit both lake types.

Results from experiments in other aquatic invertebrate assemblages suggest similar mechanisms structuring communities. For example, zooplankton assemblages in high altitude ponds in the Rocky Mountains show patterns of organization similar to the damselfly system (Dodson 1970, 1974, Sprules 1972). *Daphnia rosea* and *D. middendorffiana* segregate between ponds that have alternatively *Ambystoma* salamanders or *Hesperodiaptomus shoshone* copepods as top predators. In spite of the strong segregation by *Daphnia* species between ponds, a small copepod, *Leptodiaptomus coloradensis,* is "ubiquitous" in both pond types (Dodson 1970). The results of Dodson (1970, 1974) and Sprules (1972) suggest that *L. coloradensis* can coexist with the *Daphnia* in each pond type, because it is better at utilizing resources but poorer at avoiding predators. In spite of experiencing high predation rates, *L. coloradensis* is the most abundant grazer for most of the summer in both pond types (Dodson 1974), suggesting that it may be more effective than the other grazers at consuming algal resources and converting them into offspring. Obviously, more experiments are required to test these ideas definitively in this system, but these results do suggest that this zooplankton system may be organized by mechanisms similar to those in the littoral damselfly system.

A broader theoretical framework which recognizes that all positions in a food web are not similarly affected by dramatic environmental alterations may also help reconcile disparities between aquatic and terrestrial systems in their responses to manipulating the top trophic level. In aquatic systems, manipulations of top species often result in dramatic food web changes that "cascade" down through the food web (e.g., Power 1990, Carpenter and Kitchell 1993). However, such responses to predator manipulations are rarely seen in terrestrial systems (Polis 1991, Strong 1992, Polis and Strong 1996). Strong and Polis propose many differences between aquatic and terrestrial systems that may account for this difference in response (e.g., they suggest that in terrestrial systems, trophic levels are less pronounced, detritus is an important source of carbon, and omnivory is more prevalent). I would suggest that differences in the distributions of various types of food web positions and thus the distributions of trade-offs faced by species across various ecological milieus may also contribute to this difference in response to predator manipulations between aquatic and terrestrial systems (see also McPeek 1996*a*).

In aquatic systems, different food webs develop primarily on the basis of the presence or absence of particular top predators, with the resource bases of these different food webs (i.e., algae) being relatively similar. In terrestrial systems differences in plant secondary chemistry are thought to influence the distributions of many herbivores (Ehrlich and Raven 1964, Rosenthal and Berenbaum 1992). However, this is not true of all herbivores; for example, many herbivorous insects display no correlation in performance when raised on different host plants, in spite of the expectation that this should entail strong trade-offs resulting from conflicting abilities to deal with various plant secondary metabolites (see reviews by Futuyma and Moreno 1988, Jaenike 1990, Via 1990). This has led many to stress the importance of ecological agents such as predators and parasitoids over plant secondary chemistry in determining herbivorous insect diet breadth and consequently structuring terrestrial insect assemblages (e.g., Jeffries and Lawton 1984, Strong et al. 1984, Bernays and Graham 1988, Holt and Lawton 1993). Interestingly, predators and parasitoids are those ecological agents that are not necessarily restricted to any particular host plant. As in other systems, coexistence of herbivorous insects feeding on plants may be facilitated by some species being better adapted to plant chemistry and others being better adapted to avoiding predators and parasitoids. If true, in terrestrial systems species that are better adapted to avoiding predators should have broad ecological distributions, and species that are better adapted to resource utilization should have more narrow ecological distributions.

If these differences between aquatic and terrestrial systems in the relative ecological distributions of species do exist, manipulations of top predators should have different consequences in them. Because the more narrowly distributed species segregate with different predators in aquatic systems, manipulations of predators often result in dramatic changes in species composition (especially if new species can colonize experimental units). This in turn causes "cascades" because alternative prey assemblages often also differ in their abilities to utilize resources; e.g., large-bodied zooplankton, which coexist with invertebrate predators, generally graze algae faster than small-bodied species, which coexist with fish (Goulden et al. 1982, Gliwicz 1990, but see DeMott and Kerfoot 1982, Stemberger and Gilbert 1985). In contrast, if in terrestrial systems the more narrowly distributed species segregate on the basis of resources and the more broadly distributed species are those that are better adapted to predator avoidance, manipulations of predators should generally alter the abundances of species but not result in dramatic changes in species composition. Moreover, the effects of these manipulations on resource-adapted species may in turn cause variable responses in plants.

Much of the controversy in the literature may be the result of not recognizing that species have differential abilities to engage in various ecological interactions, that these differences in abilities influence the scale at which various trade-offs are important, and that the scale at which various trade-offs are important differs between systems.

Given that some change in species composition is a general consequence of moving among ecological milieus, be it moving from areas dominated by physical stress to areas dominated by competition (Connell 1961, Jaeger 1971, Lubchenco 1980), from competition to predation (Paine 1966, 1974, Harper 1969), or between different predation regimes (Dodson 1970, 1974, Sprules 1972, Zaret 1980, Vanni 1988, McPeek 1990*a*, Arnott and Vanni 1993, Werner and McPeek 1994, Skelly 1997, Wellborn et al. 1996), theories exploring such changes must necessarily incorporate these effects. The difficulty in this endeavor is predicting changes in the phenotypic properties of species, but this is a critical component since the phenotypes of interacting species strongly influence the mechanisms and strengths of interactions between them. Understanding changes in food webs therefore requires that we understand not only what interactions limit or facilitate existence of a particular species under some set of environmental regimes (e.g., fish vs. dragonfly lakes, low vs. high nitrogen soils), but also how the phenotypes of species determine these outcomes, and how species came to possess the phenotypes they express today. Attempts at incorporating this more evolutionary perspective into community models (Ricklefs 1987, Tilman 1988, Brown 1992, Abrams and Matsuda 1993) and empirical inquiries of the role that evolution plays in structuring communities (Losos 1992, 1994, Benkman 1993, Peckarsky et al. 1993, Scrimgeour and Culp 1994, McPeek 1995, 1996*b*, McPeek et al. 1996) are beginning, and this expansion of perspective and focus will lead to a better understanding of biological communities.

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